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THE FIXATION OF CHARACTER IN ORGANISMS[1]

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THE segregation of animals and plants into those groups which we call species, genera and families and the arrangement of such groups in a natural system of classification are made possible by the fact that during the evolution of any group there are always characters which have varied comparatively little and, from their constancy throughout large numbers of otherwise different individuals, are therefore of great value in determining relationships. Should all the characters of an individual be equally subject to change in the passage from one generation to another such chaos would result that anything but the most arbitrary classification would be quite impossible. It is of great importance to the taxonomist, the experimental morphologist and the student of evolution in general to ascertain, if possible, what are the causes for these differences in degree of variability and to attempt a formulation of the laws under which they appear.

The first attempt at a scientific explanation of this problem was put forward by the theory of Natural Selection. In its extreme form this theory assumes that all conservative characters, known to be very ancient because of their occurrence throughout large groups of organisms, are characters of supreme importance in the

[1] Graduate Bowdoin Prize Thesis in Biology, Harvard University, 1913.

struggle for existence, which have consequently been firmly standardized and kept rigidly true to type by the action of natural selection in continually eliminating those individuals which showed a tendency to depart from the normal condition. The invariable presence of segments in the Articulata, of tracheæ in insects, of the backbone in vertebrates, of gills in fishes, of feathers in birds, of roots in the vascular plants, of seeds in the spermatophytes and of vessels in the wood of the angiosperms, all of which are characters of universal occurrence in the groups which they distinguish, is explained as due to their supreme importance for survival. The frequent variability of rudimentary or obviously useless structures is laid to their unimportance in the struggle for existence and their consequent removal from the standardizing influence of natural selection. This belief in the dependence of structural conservatism on functional utility is widely held to-day and has been stated by Montgomery as follows: "A character which persists through a very long racial period must do so by virtue of being of particular value for the economy of the organization or for the perpetuation of the race. Structures of less value are more readily modified, substituted or even lost."[2]

A strict application of the selection hypothesis, however, evidently fails to explain many facts which a study of phylogeny brings forward. Can we imagine, for example, that either the number five, on which echinoderms are built, or the number three, which is characteristic of all hexapod insects, are or ever have been of critical value in the struggle for existence? Is it logical to suppose that the position of the protoxylem with reference to the later-formed elements of the vascular axis, a position which is extremely constant throughout the main groups of vascular plants, has been definitely determined by natural selection, or that the precise number of floral parts or the

[2] Montgomery, T. H., "On Phylogenetic Classification," *Proc. Philadelphia Acad. Sci.*, Vol. 54, 1902, p. 214.

particular degree of coalescence or adnation exhibited between them, is of great functional importance? Many structures, insignificant and in all probability quite useless, are extremely constant throughout large groups of animals and plants. Must we believe that all these conservative characters and structures are of immense importance in the struggle for existence, but that such features as size, shape, color and texture, which are comparatively inconstant, are of much less survival value? It is true that certain discoveries of modern physiology have lent some support to the oft-repeated defence of the selection theory that structures of apparently little importance may be in reality of much significance to the organism. Our knowledge of vital processes is as yet so slight that it is quite impossible to pronounce any particular feature as certainly of great or of little value for survival, but the mass of such information as we have acquired from a study of anatomy, physiology and ecology points decidedly to the conclusion that it is precisely those characters of little importance to the organism which are usually most conservative.

It is also very doubtful if the constancy of such apparently more essential characters as the vertebral column of vertebrates, the feathery covering of birds, or the floral reproduction of seed plants is due to the supreme importance of these characters in the struggle for existence, as the selection theory postulates; for it is evidently not the mere presence of a backbone or of feathers or of flowers *per se* which is of great significance to the individual, but the presence of these structures in very specific size, shape, texture, color and other respects. The vertebral columns of a shark and of an elephant could not be exchanged without disaster, nor could the feathers of a duck and an ostrich or the flowers of a pine and an orchid. The "conservative" character is useful only as it is associated in each individual with many other "variable" ones. The most fundamental and unalterable distinction between a fern and a flowering plant resides in their

respective methods of reproduction; but in a competition between the two it is not primarily this difference which decides the outcome. Differences in vegetative characters, as well, and in the general vigor and adaptability of the two plants determine which shall survive. One of the most conservative and deeply-seated distinctions between a mammal and a bird is the possession of hair by one and of feathers by the other, but in the struggle for existence between a bat and a night-hawk this difference is of very slight importance. The victor in such competitions is that individual all of whose bodily parts in their size, shape and general structure are so well coordinated as to produce an organism with the greatest degree of hardiness and adaptability.

The conservative characters in each family or larger group—its most important distinguishing features—provide a general plan of structure, a theme, on which are produced the modifications of genera and species. It is these modifications, involving the plastic and least conservative characters, which are of most importance in adaptation and therefore in survival. The general plan is of comparatively little significance in a contest—about as much as is the particular make of modern rifle used by an army or the special type of construction of a racing car. A satisfactory interrelation and coordination of parts is the important thing, and the degree of perfection with which this is attained, on almost any plan, determines success or failure. It is true that after very long periods of time in organic evolution slight differences in value between two general plans of structure will sometimes make themselves felt and the best will finally become dominant. Seed plants have little by little overcome vascular cryptogams and mammals have superseded reptiles. A highly adaptable organism, however, constructed on an "inferior" plan will often supplant one which belongs to a generally superior type but is lacking in versatility and vigor. The common bracken fern, for example, a cryptogamous plant, is of almost universal

distribution and is much more successful than most seed plants. The great majority of fundamental distinctions and conservative characters seem to be of as little survival value as is pentamery to the echinoderms or the presence or absence of stipules to any family of the dicotyledons.

The theory of natural selection, at least in its extreme form, can not therefore well be regarded as a satisfactory explanation for structural conservatism. Darwin himself frequently called attention to the fact that "the physiological importance of an organ does not determine its classificatory value"[3] and cited many examples of organs or characters obviously insignificant or useless which are nevertheless very constant and of great value in determining relationships. Darwin voices the general defence of selectionists on this point, however, when he states that "the importance, for classification, of trifling characters mainly depends on their being correlated with other characters of more or less importance."[4]

If the conservatism of a useless character depends on its correlation with one of great functional value which is continually preserved through the action of natural selection, it ought to be possible to discover this essential character and to use it in classification. A search for such universal and vitally important distinctions, however, is strangely fruitless, for in most families the only characters which we can definitely point out as common to all the individuals are precisely those which seem utterly insignificant for survival. This fact becomes increasingly obvious as we consider still broader groups where the number of common characters becomes smaller and smaller until there are but one or two features of absolute diagnostic value. The two great divisions of the amniotes, for example, the Sauropsida on the one hand and the Mammalia on the other, can be rigidly distinguished from one another only by the presence, respect-

[3] "Origin of Species," 6th ed., p. 431.

[4] *Loc. cit.*, p. 433.

ively, of one or of two occipital condyles or joints between skull and backbone. The two largest families of living conifers, the Abietineæ and the Araucarineæ, are roughly separable on several characters, but the only distinction to which no exception has been found is the presence or absence of "bars of Sanio," minute bands of pectose on the walls of the wood elements. Similarly, the monocotyledons and dicotyledons, the two great divisions of the higher seed plants, are ultimately separable, as their names imply, by the number of the cotyledons in the embryo. It can not well be claimed that any of these characters or many others which are common to wide groups of animals and plants are in themselves physiologically important but it is equally impossible to distinguish others, of great value for survival, with which these are correlated.

Darwin frequently calls attention to the fact, now so generally admitted, that a classification based on one or a few distinctions is of much less value than one which takes into account a large number of correlated characters. Such a group of characters, however, corresponds to what we have mentioned as the general plan or type of structure and consists, at least in the broader groups of organisms, of features which are mainly unimportant for survival.

It is possible to maintain that the success or failure of an organism depends more on some deeply seated property of its protoplasmic make-up, such as its powers of resistance or adaptability, than on any external and visible structures. But if there is a correlation of such fundamental abilities with features of structure, is it not more reasonable to suppose that it would occur with characters of great functional importance rather than with those which are of no physiological significance? The fact that so often in the same family, all of whose members possess the typical conservative features of the group, there are some individuals which are dominant and successful and others which are unsuccessful and are

being exterminated seems to prove that there is no correlation between the vigor and adaptability of the organism and its conservative structural characters.

Darwin maintains that the constancy of useless features "chiefly depends on any slight deviation not having been preserved and accumulated by natural selection which acts only on serviceable characters";[5] but if all the characters and structures of any particular group were originally variable in the same degree, a supposition which the theory of natural selection is usually regarded as making, it is surely impossible to suppose that variations will not be most strikingly manifest in just those features which are not subject to the eliminating action of natural selection.

Simple and plausible as the selection theory is, we must admit that it offers by no means a complete solution of the problem of fixity since, in general, the conservatism of a structure or character seems to be inversely rather than directly proportional to its survival value. To reach a better understanding than such a theory gives as to why variation does not occur with equal frequency and extent throughout all parts of an organism, we must first of all endeavor to formulate, from the great mass of facts at hand, such general laws of variability and conservatism as we may be able to discover empirically and must then try to explain them as well as we may. A survey of the fields of taxonomy and comparative anatomy shows the possibility of discovering in the evolutionary development of organisms the presence of numerous uniformities and the operation of many general principles of phylogeny, some of which are of universal occurrence, or nearly so; others valid throughout large groups of animals and plants, and still others applicable only to particular orders or families. The formulation of such principles and a thorough application of them is the great task before the taxonomist and the phylogenist, if they are to establish their sciences on a sound and rational

[5] *Loc. cit.*, p. 431

basis as something more than mere collections of facts. The purpose of the present paper is to set forth a few of the more important of these evolutionary principles, with their significance in the general process of evolution, and to suggest a possible explanation for the fixation of character which shall be more satisfactory than that proposed by the selection theory.

In our search for such principles of conservatism, it is primarily apparent that in the main those features which are slow to change in one family are slow to change in others also, and that consequently there are certain rather definite categories of characters which throughout all animals and plants show an inherent tendency to be conservative and slow to change, and others which are fundamentally plastic and variable. The conservative categories are, in general, those of number, relative position and general plan, characters usually of little functional significance; whereas the commonly variable features are those of more importance for survival and include such distinctions as size, shape, color and texture. The essential difference between these groups of categories is not at all in their absolute degree of conservatism or plasticity, but rather in their general tendency to become fixed or to remain plastic. Number, position and plan are not always constant, by any means, but they tend to become so during the course of evolution, whereas size, shape, color and other commonly variable characters are almost always changeable and rarely become stereotyped.

The conservatism of number is everywhere apparent. The two great groups of radially symmetrical animals, the cœlenterates and the echinoderms, are constructed (with a few exceptions) on the plans of six and of five, respectively. Insects, on the other hand, display almost invariably a scheme of three or its multiples in the number of body regions, segments, appendages and many other structures. Among fishes the number of gills, of visceral arches, of fins and of fin rays varies little throughout large families; and in the higher vertebrates, the number

of teeth, of vertebræ, of digits, of aortic arches, of brain lobes, of cranial nerves and of countless other structures is very conservative and is characteristic of large groups of animals. In the plant kingdom the fixity of number is even more noticeable. Throughout gymnospermous plants the number of sporangia to a sporophyll, in both the male and the female cones, varies but slightly. The two great groups of angiosperms, the dicotyledons and the monocotyledons, can be separated on but one constant character, the number of cotyledons in the embryo. The numerical plan of the flower in both series is also very constant, being almost invariably four or five in the dicotyledons and three in the monocotyledons. Most angiosperm families, or genera, at least, have a characteristic number of sepals, petals, stamens and carpels, which is of great importance in classification. Similar instances could of course be multiplied almost indefinitely.

Conditions of relative position and of insertion of parts are also notably conservative and of value in determining relationships. In the higher invertebrates, for example, the nerve cord is always ventral to the digestive tube and chief blood vessels, whereas in the vertebrates it is invariably dorsal. The mass of the liver may be disposed almost anywhere, but its attachment is always on the ventral side of the digestive tube. The source of the nerve supply to many organs is exceedingly slow to change and is of much importance in determining the primitive position of structures which have been moved from their original situation. Among plants, the relation of bud to leaf is very constant, and the particular relative positions of sporangium and sporophyll, of protoxylem and later-formed wood elements, and of parenchyma cells and vessels are very characteristic for each of the main groups of vascular plants. The degree of coalescence between the members of the same floral circle and the method of insertion of each of the floral circles upon the axis or upon one another are admitted to be of the greatest diagnostic value.

The character of general plan, or type, which really includes those of number and position, is of the utmost importance for the discovery of relationships. In every natural group of organisms, no matter how dissimilar its members may appear, there is always a specific plan or theme which is common to all and upon which the structure of each individual is built. The two-layered or three-layered body plan, the presence or absence of segmentation, the definite type of arthropod or vertebrate appendage which is so constant throughout its endless modifications, the plan of the central nervous system in the vertebrates, and the precise and unvarying character of the epidermal structures in the different classes of that phylum, are a few of the innumerable examples of the conservatism of type in the animal kingdom. In the case of plants the same fact is no less evident. The general topography of the vascular system, the presence or absence of leaf-gaps, the degree of differentiation in the structure of the wood and the open or closed character of the leaf venation are all extremely constant. The notable conservatism of type in the reproductive organs of all plants is well known and is universally used in classification. The almost complete uniformity throughout animals and plants of many cytological characters, such as those concerned with mitosis, might also be cited as striking examples of the conservatism of plan or type.

Plastic and variable characters, no less than conservative ones, are separable into categories, the most important of which are size, shape, color and texture, of which the inconstancy is so notorious that any broad classification based upon them is very rarely a natural one.

But even if we admit that certain characters are essentially more slow to change than others, it is very evident that this difference is not an absolute one, but that "conservative" features may display a greater or a less degree of constancy in certain parts of the organism than in others. These differences in local variability, however, like those between general categories of characters, are

not random and entirely unpredictable ones, for we are able to distinguish certain definite parts of the plant and animal body which throughout larger or smaller groups of organisms are characteristic seats of conservatism, and others which are everywhere subject to continual change. The urinogenital, nervous and skeletal systems of vertebrates, and to a certain extent of invertebrates as well, are typically conservative and subject to comparatively slight alteration during evolutionary development. Certain definite regions of the body, such as the skeleton of the mammalian neck, are more definitely stereotyped than others as to the number and arrangement of parts. The extreme conservatism of the reproductive organs of all plants has of course long been recognized and has been proven by a study of internal as well as of external structure. More recently it has been demonstrated, that the woody axis, as well, is the seat of firmly fixed and therefore ancient characters. Each main division of the vascular plants has a fundamental stelar plan, and every subordinate group has its peculiar and specific type of wood structure which is exceedingly constant in individuals otherwise very different and, as a diagnostic character for families and sometimes smaller groups, is therefore of much value. The axis of the root is especially conservative and has remained practically unchanged in its general plan throughout the entire evolution of woody plants. The vascular system of the leaf, especially at the node where the leaf and stem unite, has many times been found to display primitive features wholly lost elsewhere. In such conservative systems and regions it is not *all* the characters which have become constant, but only those which we have called typically conservative, such as number, position and plan. Variable characters are variable anywhere.

Not only are certain regions of the body characteristically more conservative than others, but it is also true that particular stages, notably the earlier ones, in the life history of the individual are much less subject than the

rest to variation and change. The law of recapitulation, which declares that ontogeny repeats phylogeny, is now accepted in a more or less modified form by almost all zoologists, and despite differences in the interpretation of embryology as a guide to a knowledge of ancient animals, it is generally agreed that early developmental stages are much more conservative than are later ones.

Not as many striking examples of recapitulation are known among plants as among animals, but Darwin long ago noticed resemblances between the leaves of certain seedlings and of their supposed ancestors, and others have cited many similar instances. Attention has more recently been called, particularly by Jeffrey, to the fact that the internal structure of the young plant or of a first annual ring of the mature plant, even more clearly than their external form, is slow to change and therefore frequently displays primitive characters. The woody axis of one of the higher ferns begins in the sporeling as a solid rod, which, after forming a medullated cylinder, gives rise to the complicated vascular system of the adult, the various steps of its development representing stages through which its ancestors doubtless passed and which now characterize the more primitive living families of ferns. In the first annual ring of certain conifers occur resin canals, "bars of Sanio," parenchyma cells and other structures present throughout the wood of more primitive and presumably ancestral types. The first few annual rings of many angiosperms, as well, show in the structure of their rays and vessels characters which are undoubtedly ancient. On an abundance of such evidence as this it must be admitted that the validity of the law of recapitulation has been demonstrated for plants almost as thoroughly as for animals.

We have seen that conservative characters vary considerably in their constancy according to the part of the body or the stage of development with which they are associated. Still more notable cases of differences in fixity are evident in similar characters occurring in different fami-

lies. A feature which is conservative and of diagnostic value in one group may be variable and worthless in another. The number of teeth and vertebræ, for example, is much less constant among fishes than among mammals. The general floral plan is far from uniform throughout the Rosaceæ, but in such families as the Cruciferæ it is exceedingly constant. This introduces still another principle of conservatism which is really the crux of the whole problem of fixation of character and seems to be a fundamental law of evolution—the principle that the progressive evolution of any character or structure, whether involving reduction or increased complexity, is attended by a continual decrease in its tendency to change. Differentiation and specialization are followed by increasing fixity.

It is a well-known biological fact that the more primitive families of animals and plants, those which still maintain an ancient type of organization, are much more variable in their characters than are those which have progressed far from such a primitive condition. The lower Arthropoda, for example, display great variety in the number of body segments and appendages and in many anatomical features, but the highly specialized hexapod insects, despite their enormous numbers, wide distribution and extreme variation in size, shape and color, have become rigidly stereotyped with regard to almost all characters of number and general plan. In the ascending vertebrate series from cyclostomes to mammals there are also many instances of the increasing fixation of what we have called conservative features, for it is well known that the characters which make up the mammalian type are much more definite and sharply circumscribed than those pertaining to the lower groups of vertebrates where there is much latitude in the distinguishing features. Likewise, the most advanced and highly specialized families of plants, such as the Compositæ and the Orchidaceæ, are characterized by a stereotyped floral plan which is invariable throughout all the members of these dominant groups, whereas in plant orders admittedly lower in the scale, such as the

Rosaceæ, Caryophyllaceæ, Cyperaceæ and Gramineæ, the floral type is very much more various both in number and in relative position of parts. The evolution of the gametophyte from its gymnospermous to its angiospermous condition is a continual progress from simple and variable structures to those which are fixed and highly specialized. The same principle is evident as well among vegetative structures, for the lower and more "generalized" families, both among conifers and dicotyledons, show a greater diversity in their wood structure than do the higher groups.

This progressive evolution from a primitive variable condition to one which is fixed and specialized is always attended by a reduction in the number of similar parts. Multiple structures are characteristic only of the lower types of organization. Other characters tend to show a similar phylogenetic change from the complex to the more simple, with the result that a structure in its highly developed state is very often less complex than is its more primitive homologue. Evolution more often involves reduction than amplification.

These four general principles of conservatism—that there are definite categories of fundamentally conservative and fundamentally variable characters; that certain organs or regions of the body are more conservative than others; that early stages in ontogeny are more constant than later ones, and that advance in evolutionary development involves an increase in fixity, are established on a large and continually increasing mass of observed facts and may well demand recognition from all biologists. Many other principles, such as those concerned with reversion and orthogenesis, are gradually being formulated and it is only a matter of time and more extended observation before the science of phylogeny will be placed on a much more uniform and exact footing.

To establish these laws on a sound basis of observed facts is a matter of some labor, but it is a much less difficult undertaking than to provide a reasonably complete

explanation for their existence. This task must ultimately be left to the sciences of physiology and genetics, and in the meantime it is possible only to make suggestions and conjectures as to what are the causes which underlie the facts of conservatism.

The very difficulties in the way of the explanation of fixity proposed by the theory of natural selection suggest a possible solution of one of the most conspicuous problems—why it is that just those characters of least physiological importance and survival value are most conservative. May it not be true that the tendency toward progressively increasing fixity, which seems to be almost universal in organic evolution, has succeeded in rendering comparatively invariable those features which are of little significance for survival, but that in the case of vitally important characters this tendency has been overcome by the opposing action of natural selection in eliminating individuals which are not sufficiently plastic and adaptable, and in thus maintaining or increasing the variability of all characters important in the struggle for existence?

If this conception of the matter is a true one, the function of natural selection is almost precisely the reverse of what it is ordinarily supposed to be, for instead of operating to fix characters and preserve types intact its action results in their elimination, in so far as they interfere with success, and in the placing of a premium on versatility. Selection, in other words, is made for general adaptability under varying conditions rather than for the possession of any particular characters or structures. The great variability of dominant organisms, long ago noticed by Darwin, should be regarded on such a hypothesis as a cause rather than a result of their dominance. Fixity is tolerated by natural selection only so long as it affects characters of little or of no functional importance. Such characters thus become very conservative and furnish the taxonomic "type." This conception of organic evolution as the result of the continual inter-

action of these two great factors—progressive fixation, which is ever tending to make characters constant and to decrease variability; and natural selection, which operates in eliminating individuals which have become too rigid in their vitally essential features, and thus in encouraging those which display superior adaptability—is at least helpful in presenting a clear picture of the process of evolution.

The marked conservatism which we have noticed in particular structures or organs may perhaps be explained in a similar way as due to their comparative unimportance in the economy of the individual. The fact that the reproductive organs in all plants and in many animals are especially conservative may possibly be taken to indicate that the particular method of reproduction is of less vital concern to the race than are its other activities. The conservatism of other structures, such as the root, is evidently due to the comparative constancy of their surroundings. Internal structures in general are apt to be more conservative than external ones because of their exposure to a less varied environment.

Various attempts have been made to explain those phenomena of conservatism which have been grouped under the head of recapitulation. De Vries has maintained that the seedling characters of plants are just as dependent on the action of natural selection as are those of the adult and that ancient features persist in youth only when they happen to be of survival value for the early stages of the plant. The same position has sometimes been maintained on the zoological side. To attribute functional importance to all embryological characters, however, and to explain the numberless cases where there is close correspondence between ontogeny and ancestry as due simply to the operation of natural selection, is to burden that hypothesis beyond all necessity.

The theory of formative stimuli, which explains the persistence of structures in the embryo of animals on the assumption that their presence is absolutely necessary as

a "stimulus" for later development, meets with difficulties in the case of plants. Here development is not due to interstitial growth, as in animals, and does not involve progressive differentiation of almost all the cells of the body, but is brought about by the activity, at a growing point, of a small group of undifferentiated, continually dividing cells, from the innermost of which are laid down tissues which almost immediately become fixed and unalterable in size and shape. The influence, upon such a distant growing point, of structures previously laid down must be slight as compared with the effect of already formed structures, in animals, upon growth in which they themselves are taking an active part.

The facts of recapitulation can perhaps be understood better on the principle, which we have already discussed, that certain categories of characters are inherently more conservative than others. It may be said that, theoretically, every individual tends to inherit all the peculiarities of its ancestors; but since life is short and history is long, most of the chapters have to be omitted. It is only reasonable to suppose that those features will disappear first during evolutionary advance which are least conservative and least firmly fixed in the constitution of the race; and such we find to be the fact, for it is not characters of size, shape, color and texture which are usually preserved in ontogeny, but the less plastic ones of number and plan. The presence of gills and their associated skeletal and circulatory structures became rigidly implanted in the primitive vertebrate stock and the general outline of these structures still persists in the embryos of modern terrestrial forms. It is not a functional gill which is repeated, however, nor one of definite shape or special construction, but simply a gill cleft, with the vestiges of its ancient skeleton and vascular supply. It is as though what the geneticist would call the factor for the gill openings had persisted unchanged, but that the factors for the shape, size and structure of the gills had been widely altered or disappeared altogether. The developing axis

of a woody plant repeats little of the histological features of its predecessors, but it does recapitulate the general vascular topography of successive ancestral forms. The developing organism has concentrated within it an essence, so to speak, of the most conservative and therefore the most salient characters which distinguished the ancient members of its line. The fact that all plastic and highly variable features have been swept away enables these historical landmarks to stand out distinctly, and gives to the structure of the animal embryo and of the young plant a very important significance in the science of phylogeny.

The principle that fixity of character increases with differentiation, which we have regarded as of so much importance in evolution, is easier to establish than to explain. It is possible to regard the matter from the viewpoint of genetics and to imagine that a "variable" species is a "mixed population," the members of which are continually intercrossing, and that the appearance, in certain individuals, of definite discontinuous variations isolates such individuals from the rest of the species and causes the partial or complete establishment of each as a distinct "pure line" with more closely defined characters. The more numerous such discontinuous variations were, the more complete the isolation of a given line would become and the more purely, therefore, would it reproduce itself until finally its characters became very sharply fixed. In other words, fixity may be due to germinal segregation and may depend directly on the proportion of factors which are in a homozygous condition in the germ plasm of the two parents. Complete homozygosity in both would ensure complete fixity of parental characters in the offspring.

A comparison also suggests itself between the effects of differentiation in ontogeny and in phylogeny. Experimental work has shown that in the more primitive animals, where the power of regulation is best developed, any part of a tissue or elementary organ, so long as it remains

undifferentiated, is able, upon necessity, to give rise to all structures that the whole tissue would normally have produced. A sufficiently large group of cells from any portion of the blastula of an echinoderm, for example, will produce a normal larva; but the moment the process of gastrulation begins, this power of producing the whole animal is definitely lost by those very cells which possessed it but a few hours previously; for, now that differentiation has begun to take place, a piece which shall give rise to a normal larva must include a little of both the primitive ectoderm and entoderm and can not be taken at random from anywhere in the embryo. Any portion of the primitive gut, which later develops, is able to produce the cœlomic pouch, should the normal region of origin of that structure be removed, but this "equipotency" lasts only so long as there is no differentiation, for if the pouch once begins to develop and then is removed it can never be produced again even by the cells which a short time previously had the power to form it. This process of ontogenetic segregation results in the continual loss of potentialities, in the progressive narrowing down of the possibilities at the command of every living cell. The situation in phylogeny is very similar, for the possibilities before a simple, plastic and comparatively undifferentiated organism—the lines of evolution along which its descendants may go—are much greater than those before one which is highly developed and sharply specialized. Increased differentiation is followed so regularly by decreased plasticity, both in phylogeny and ontogeny, as to suggest the possibility of a common cause.

There is also a similarity between structural fixation and certain psychological phenomena. The performance of an action is always uncertain and variable at first, but constantly tends to become stereotyped and habitual. The simpler types of animal activity are directed by instincts which are comparatively changeable and plastic, but where behavior has become highly specialized and complex, in-

stinct has attained a high degree of precision and invariability. In the same way, a person whose activities are of wide range and comparative simplicity is much more adaptable than one who has become habit-bound through a life of intense specialization. As an organism's "experience mass" becomes continually greater and more complex the formation occurs of that system of habits which in man we call a mental character, and this process, like that of ontogenetic and phylogenetic development, involves the continual elimination of potentialities and consists in the progressive fixation, with advancing age, of characters which during youth were variable and inconstant. It so much resembles the establishment of an organic structural type by the elimination of variability through advance in specialization as to suggest that perhaps both phenomena are manifestations of the same cause.

Such attempted explanations of the differences in fixity which occur between organic characters are of course incomplete and highly unsatisfactory. The very fact, however, that it is possible at all to formulate principles of conservatism and variability, unexplained though they may be, which shall be of application throughout the animal and plant kingdoms or which shall at least be operative in certain definite groups of organisms, is of great significance and value to the biologist, for it enables him to place all branches of his science on a somewhat more exact and uniform basis. It must of course be borne in mind that such principles as these are not invariably operative, for exceptions to all of them are frequently found. Biological laws undoubtedly exist, but they seem to belong to quite a different category from the invariable ones of the physical sciences.

The science of taxonomy will perhaps receive the greatest benefit from a general recognition of the fact that there are such things as laws of phylogeny, for a united effort by all biologists to define these laws more clearly and to apply them more widely will result, through the

establishment of much more precise taxonomic criteria, in a clearing up of many difficulties and disputes as to relationships and in the construction of a truly natural classification on a more logical and consistent basis.

A knowledge of phylogenetic principles is also of value to the general student of evolution, for through it a better conception of the development of organic structures may be obtained than is set forth by the selection theory. A recognition of the facts that fixity increases with differentiation and that there are inherent differences in variability between functionally important characters and those which are useless for survival makes possible a much clearer understanding of the evolutionary history of any particular group.

The evolution of the hexapod insects is a case in point. The primitive insects seem to have been air-breathing arthropods with an indeterminate number of body segments and appendages. The ancestors of our modern hexapods achieved their first success through some advance in specialization over this more primitive type, but the improvements which gave them ascendancy and which enabled them to found a distinct and dominant group were certain unknown changes, doubtless in plastic and functionally important characters which were of great value for survival at the time, but which, having isolated the family and put it on its feet, so to speak, continued to change and may be possessed by few or no living descendants. The progressive increase in specialization, however, which caused the success of the primitive hexapods resulted in the gradual fixation of certain functionless characters, such as the number of segments and appendages, which finally became rigidly stereotyped as we see them to-day, so that they now distinguish *all* hexapods, whether successful and dominant species or those which are being beaten and exterminated. The conservative features have progressed steadily but slowly to their present condition, but the plastic characters, during the same time, have doubtless passed through wide and unre-

corded ranges of variation and in so doing they have, as it were, caught and fixed into the advancing and increasingly specialized hexapod type the particular conservative and functionless characters which happened to distinguish those fortunate individuals which founded the present family. As a result our modern hexapods, as a whole, like all other natural orders, have as constant characters certain peculiarities of number and plan, whereas the subordinate groups of the order are still distinguished, in many cases, by the functionally important features to which they owe their successful establishment, but which in future evolution are doubtless destined to vary much.

Similarly, in that ascending group of animals which were to give rise to the higher vertebrates, the primitive archipterygium became stereotyped into the pentadactyl appendage, with its definite skeletal plan; but the particular improvements which caused the primitive pentadactylous stock to succeed at the start and to become segregated as a new and distinct order were doubtless concerned with such plastic but functionally important characters as size and shape and with the general vitality and adaptability of the race, and had little or nothing to do with the particular number of digits or arrangement of bones in the appendages. These characters, originally variable, simply happened to belong to a successful and progressive group of organisms and became fixed and stereotyped as specialization took place.

The ancestors of the grasses doubtless varied much as to nodal structure, but the particular group which through its success became the dominant and distinct modern family happened to be characterized by the possession of leaves whose bases formed an open sheath around the stem and were provided with a small membranous structure, the ligule. These characters, which are doubtless not the ones to which the family owes its success, since they are present alike in dominant and in unsuccessful species, became so firmly fixed during the progressive evolution of the Gramineæ that they now distinguish all members of the family.

All conservative and stable characters which are common to large groups of organisms have thus reached their present condition through slow but steady progress during the same time that plastic and functionally important features were changing and moulding themselves in adaptation to every new demand of the environment.

Organic evolution in general, including that of human civilization, seems to have resulted from the opposing actions of the two great factors which we have so often mentioned: on the one hand, the tendency toward fixation, which results in the stereotyping of structures and of habits and social customs, and which gives rise to mental as well as physical conservatism; and, on the other, the action of natural selection in weeding out such physical characters as tend to make the organism unadaptable and such customs, institutions and even societies as have become too firmly stereotyped through habit and precedent or too bound by tradition to maintain themselves in the advance of civilization. Natural selection does not interfere with useless or harmless characters which therefore become firmly fixed and are of great value in determining relationships between organisms and between civilizations and in deciphering the path of evolutionary advance.

This biological principle that trivial but conservative characters which happen to distinguish the beginnings of a successful evolutionary line become closely associated with all its subsequent development has therefore many suggestive parallels in human history. Any great movement is always colored by the circumstances surrounding its inception. The fact that our first popular translation of the Bible happened to be written in the seventeenth-century English does not account for the enormous subsequent spread of the Scriptures, but nevertheless the now archaic phraseology of the King James Version, a "conservative character" like all religious phraseology, and "unimportant for survival," has persisted almost unaltered throughout the history of the Protestant churches,

and, surviving numberless changes of ritual, creed and theology, has stamped itself indelibly upon religious expression everywhere.

The whole subject of organic conservatism is so vast and so little understood as to be far beyond satisfactory treatment within the limits of such a paper as the present one. An extensive correlation of the mass of facts already in our possession and the discovery of a multitude of new ones will be necessary in order to formulate laws of phylogeny with any degree of accuracy. The essential point in the whole matter is the indication that evolution of animals and plants is not a random and fortuitous process, dependent on the caprice of external, inorganic nature, but that it is subject everywhere to certain definite and discoverable laws. Such a point of view, of course, is essentially an orthogenetic one and emphasizes the importance of the evolving organism rather than the creative power of the environment. By establishing the essential uniformity of vital processes everywhere it also tends to elevate biology from a mere subsidiary of the physical sciences to an independent position of its own.

Summary

1. The construction of a natural classification of organisms is made possible only by the fact that certain characters of every individual are more conservative and less subject to variation than others during evolutionary development.

2. The explanation of conservatism propounded by the theory of natural selection is unsatisfactory since, so far as we are able to determine, characters which are most firmly fixed are in general those of least importance for survival.

3. From a study of phylogeny it is possible to formulate certain general principles of conservatism which are valid throughout more or less extensive groups of organisms.

4. The principal categories of conservative characters are those of number, position and plan.

5. Particular organs or regions of the body, throughout large groups of animals and plants, are less subject to change than others and hence are seats of primitive characters.

6. The early ontogenetic stages of animals and plants repeat those characters which were most conservative and firmly fixed in their ancestry.

7. Evolutionary advance and increase in differentiation tend to result in the decrease of variability. This is analogous to the loss of potentialities during ontogeny and is also comparable to the formation of habit.

8. Organic evolution is dependent on the action of two opposing factors: that of progressive fixation, which tends universally toward greater rigidity and conservatism in all characters during evolutionary advance; and that of natural selection, which tends to maintain or increase the variability of those characters important for survival by eliminating individuals where such characters have become so fixed that the organism fails to possess a necessary degree of adaptability. Natural selection is not concerned with harmless and trivial characters which consequently tend to become very conservative and are of much value in classification.

9. Such general principles of phylogeny as these, if thoroughly established and defined, will make possible the construction of a truly natural classification of organisms on a logical and uniform basis. They also present a clearer conception of the general method of evolution than is set forth by the theory of natural selection alone.

The writer is much indebted to Professor Herbert W. Rand, of Harvard University, for suggestions and information.

INHERITANCE OF LEFT-HANDEDNESS[1]

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Introduction.—The fact that left-handedness "runs in families" has probably attracted the attention of many observers, yet the method of inheritance has not been fully studied. Many people imagine the condition to depend entirely upon training or imitation. There is thus much of guesswork concerning the true nature of the condition.

Literature.—A considerable bibliography of left-handedness has recently been cited by Professor H. E. Jordan.[2] Most of his references are, however, to articles of little value, especially since nearly all of them were written previous to the modern period of genetic study. Professor Jordan puts forth the tentative opinion that left-handedness is a recessive character. Unfortunately the data which he presents consist chiefly of a few selected pedigrees from which the reader can obtain very little information. He suggests more than once that some of his cases are examples of the spontaneous appearance of left-handedness in a family. If such spontaneous development were so frequent the whole population would, in a few generations, be left-handed. The appearance of a left-handed child in a family without left-handed ancestors for three or four generations is not to be considered remarkable, for this is the way in which recessive characters frequently behave.

Method of Obtaining Data.—At the beginning of a course of lectures on heredity in the University of Colorado in 1911 I distributed papers calling for informa-

[1] An earlier paper, entitled "Mendelian Proportions and the Increase of Recessives," which grew out of my studies on inheritance of left-handedness was published in the American Naturalist, Vol. XLVI, pp. 344–351, June, 1912.

[2] *Breeders' Magazine*, Vol. II, pp. 19–29 and 113–124, 1911.

tion from the students in regard to right- and left-handedness in their own families or in other families with which they might be quite familiar. Each student noted down the parents and every child in the family. Since the students who reported are from ninefeen to twenty-five years of age, the probability is that their families are now complete as to the number of children. Similar data were collected from another set of students in 1912. In addition to these collections of statistics, I have also studied the affection in a family of four generations, including about thirty people. Since this material offers nothing especially different from that gathered from the students, I have not included it in the present study.

TABLE I

STATISTICS OF PARENTS AND CHILDREN

	Number	Per Cent. Observed	Per Cent. Expected $4RR:4Rr:rr$	Per Cent. Expected $9RR:12Rr:4rr$
Total parents..........	610			
Right-handed parents...	561	91.94	89.99	84.00
Left-handed parents....	49	8.06[3]	11.11	16.00
Total children.........	1,130			
Right-handed children ..	953	84.34	89.99	84.00
Left-handed children....	177	15.66[3]	11.11	16.00

Value of Different Data.—Since the young people from whom the information was obtained would be much more likely to know of left-handedness among their brothers and sisters than in their parents, the reports for children are probably more accurate than those for parents. It is easy to see how a child would report a parent as right-handed unless the person were very definitely left-handed. A child would not know about the early history of his father or mother. On comparison of the number of left-handed individuals among parents and children left-handedness seems to be about twice as common among the children. This is, of course, a manifest absurdity and is

[3] Since the proportion of left-handed children is nearly twice that of the left-handed parents it is evident that left-handedness among the parents is greatly under-reported.

TABLE II

Statistics of Families

	Number	Per Cent. Observed	Per Cent. Expected $4RR:4Rr:rr$	Per Cent. Expected $9RR:12Rr:4rr$
Total families	305			
Families with both parents reported as right-handed	258	84.59	79.01[4]	70.56[5]
Families reported as having one parent right-handed, the other left-handed	45	14.75	19.74[4]	26.88[5]
Families reported as having both parents left-handed	2	0.66	1.24[4]	2.56[5]
Families reported as having all children right-handed	174	57.05	69.13[4]	59.04[5]
Families with some or all children left-handed	131	42.95	30.87[6]	40.96[7]
Average number of children per family in the population (families 305, children 1,130)	3.7			
Average number of children among families showing some left-handed children (families 131, children 548)	4.1			

[4] The expected number of matings of any particular sort, or the matings resulting in particular types of offspring, in a population of $4RR:4Rr:rr$ may be calculated from the following table:

$$\begin{array}{lrcrcr}
1. & 4RR & \times & 4RR & = & 16\\
2. & 4RR & \times & 4Rr & = & 16\\
3. & 4RR & \times & rr & = & 4\\
4. & 4Rr & \times & 4RR & = & 16\\
5. & 4Rr & \times & 4Rr & = & 16\\
6. & 4Rr & \times & rr & = & 4\\
7. & rr & \times & 4RR & = & 4\\
8. & rr & \times & 4Rr & = & 4\\
9. & rr & \times & rr & = & 1\\
\hline
 & & & & & 81
\end{array}$$

Matings 1, 2, 4 and 5 have both parents right-handed; adding $16 + 16 + 16 + 16 = 64 \div 81 = 79.01$ per cent. Matings 3, 6, 7 and 8 are each of a right-handed and a left-handed parent. Mating 9 is of two left-handed parents; this type may be expected once in 81 times, or $1 \div 81 = 1.24$ per cent. Only right-handed children will appear in matings 1, 2, 3, 4 and 7; left-handed children are to be expected in 5, 6, 8 and 9. These last make $16 + 4 + 4 + 1 = 25 \div 81 = 30.87$ per cent.

[5] The expected number of matings of a particular sort, or the matings resulting in particular types of offspring, in a population of $9RR : 12Rr : 4rr$ may be calculated as suggested in the previous footnote. Here it is necessary to use the following table:

$$\begin{array}{lrcrcr}
1. & 9RR & \times & 9RR & = & 81\\
2. & 9RR & \times & 12Rr & = & 108\\
3. & 9RR & \times & 4rr & = & 36\\
4. & 12Rr & \times & 9RR & = & 108
\end{array}$$

to be accounted for as just stated. Probably the most valuable parts of the statistics are the figures showing families with left-handed children and also the total number of left-handed children in the population.

Natural and Acquired Left-handedness.—Most right-handed people can be taught to use the left hand for many purposes, and conversely left-handed people may learn to write and perform various acts of skill with the right hand. But aside from these rather unusual cases there are many individuals who are naturally right-handed and do most of their work with the right hand. Others are left-handed by nature. Left-handedness seems to be connected with a more highly developed condition of the right cerebral hemisphere. Evidence in support of this view is found in a number of cases of aphasia connected with left hemiplegia. The left motor area of the cortex, as is well known, is associated with speech in most individuals. Hence a lesion of this area results in aphasia and paralysis of the right side of the body. When similar

5. $12Rr \times 12Rr = 144$
6. $12Rr \times 4rr = 48$
7. $4rr \times 9RR = 36$
8. $4rr \times 12Rr = 48$
9. $4rr \times 4rr = 16$

$\overline{625}$

[6] Only in the following matings could left-handed children appear:

$4Rr \times 4Rr = 12$ right-handed, 4 left-handed
$4Rr \times rr = 2$ right-handed, 2 left-handed
$rr \times 4Rr = 2$ right-handed, 2 left-handed
$rr \times rr = 0$ right-handed, 1 left-handed
$\overline{16}$ $\overline{9}$

The children in these families would then be expected in the ratios of 16 : 9, or 64 per cent. right-handed, 36 per cent. left-handed.

[7] Only in the following matings could left-handed children appear:

$12Rr \times 12Rr = 108$ right-handed, 36 left-handed
$12Rr \times 4rr = 24$ right-handed, 24 left-handed
$4rr \times 12Rr = 24$ right-handed, 24 left-handed
$4rr \times 4rr = 0$ right-handed, 16 left-handed
$\overline{156}$ $\overline{100}$

The children in these families would then be expected in the proportion of 156 right-handed to 100 left-handed, or 61 per cent. right-handed and 39 per cent. left-handed.

TABLE III

STATISTICS OF FAMILIES REPORTED AS HAVING BOTH PARENTS RIGHT-HANDED

	Number	Per Cent. Observed	Per Cent. Expected[8] $4RR:4Rr:rr$	Per Cent Expected[8] $9RR:12Rr:4rr$
Total families in the group	258			
Families within this group having all children right-handed	165	63.95[9]	75.00[10]	67.35[11]
Families within this group having some children left-handed	93	36.05[9]	25.00[10]	32.64[11]
Total children in the group	953			
Right-handed children reported in the group	837	86.74	93.75[12]	91.84[13]
Left-handed children reported in the group	116	13.26	6.25[12]	8.16[13]
Children in those families in which all children are right-handed	555	58.24[9]	75.00[10]	67.35[11]
Children in those families in which some children are reported as left-handed	398	41.76[9]	25.00[10]	32.65[11]
Right-handed children in those families in which part of the children are left-handed	282	70.85[9]	75.00	75.00
Left-handed children in those families in which part of the children are left-handed	116	29.15[9]	25.00	25.00

[8] See footnotes 4 and 5 to Table II.

[9] The figures show that some of the alleged right-handed parents are really left-handed.

[10] The population considered in this table is made up of matings 1, 2, 4 and 5 given in footnote 4 to Table II, thus:

$$\begin{aligned}
1.\ & 4RR \times 4RR = 16\\
2.\ & 4RR \times 4Rr = 16\\
4.\ & 4Rr \times 4RR = 16\\
5.\ & 4Rr \times 4Rr = 16\\
& \overline{64}
\end{aligned}$$

Obviously, only mating 5 will show left-handed children. This constitutes $16 \div 64 = 25$ per cent. of the families.

[11] The entire population considered in this table is made up of matings 1, 2, 4 and 5 in footnote 5 to Table II, thus:

$$\begin{aligned}
1.\ & 9RR \times 9RR = 81\\
2.\ & 9RR \times 12Rr = 108\\
4.\ & 12Rr \times 9RR = 108\\
5.\ & 12Rr \times 12Rr = 144\\
& 441
\end{aligned}$$

The families showing left-handed children would be only those in mating 5. This constitutes $144 \div 441 = 32.65$ per cent.

[12] The only left-handed children will be in mating 5, viz.: $4Rr \times 4Rr$. They will constitute one fourth of the children in this mating, or one sixteenth of all the children $= 6.25$ per cent.

[13] The only left-handed children will be in mating 5, viz.: $12Rr \times 12Rr$. They will constitute one fourth of the children in this mating. Hence: $\frac{1}{4} \times 144 \div 441 = 8.16$ per cent.

lesions of the right cerebral cortex result in paralysis of the left side and also in aphasia, it is sometimes found that the persons thus affected were naturally left-handed. I am informed by my colleague, Dr. O. M. Gilbert of the department of medicine of this university, that this connection of left-handedness with a speech center on the right side of the cortex is well attested.

A certain number of persons consider themselves to be "ambidextrous" and claim that they are not naturally either right-handed or left-handed. It is, however, difficult for one to know his own original condition with regard to the use of the hands, since in most homes the child is taught early the use of the right hand in taking up a spoon or cup. I suspect that the "ambidextrous" persons are really left-handed by nature.

Mendelian Explanation of Heredity of Left-handedness.—A study of the accompanying tables will suggest that left-handedness is a Mendelian recessive. It belongs to that group of characters which may show themselves in families where neither parent is affected, and sometimes in families with no affected ancestors for a number of generations. In the 305 families there are only two reported as having both parents left-handed. If the condition is a Mendelian recessive the children in these families should all be left-handed. According to the report, however, one child is right-handed. Of course it is possible that one of the parents was by nature right-handed. Possibly some heterozygous (simplex) persons may easily learn to use the left hand.

Presentation of Material.—The material collected has been classified in such manner that it can be made use of by others who may be studying the subject. In some of the tables I have indicated the expected percentages if the population were to consist of the three Mendelian types of individuals in the following proportions, viz.:

$$(a)\ 4RR:\ 4Rr:\ rr,$$
$$(b)\ 9RR:12Rr:4rr.$$

TABLE IV

BOTH PARENTS REPORTED AS RIGHT-HANDED, BUT WITH SOME OF THE CHILDREN LEFT-HANDED (FAMILIES 93, RIGHT-HANDED CHILDREN 138, LEFT-HANDED CHILDREN 116).[14]

Name of Person Reporting	Right-handed Children	Left-handed Children	Name of Person Reporting	Right-handed Children	Left-handed Children
Ahr	2	1	Max	1	1
Ba	0	1	Mer (*a*)	1	1
Bar	3	1	Mer (*b*)	2	1
Bat	3	1	Milb	1	1
Ben	3	1	Mill. L.	3	1
Br. F.	1	1	Mill. W.	6	2
Br. H.	3	1	Mur	4	1
Br. N.	2	3	N	8	1
Bu	3	1	Ol	4	1
Bur	2	1	Ow	1	1
Chr	3	1	Pe	9	3
Con	1	1	Po	2	1
Cou	1	1	Pu	7	1
D	0	1	Re	1	1
Don	4	1	Rid (*a*)	2	2
Dou	5	1	Rid (*b*)	0	1
Ed	4	1	Rid (*c*)	2	2
F (B)	3	1	Ro	4	1
F (C)	5	1	Roberts	6	2
Fl	1	2	Rbtn (*a*)	4	1
Fur	1	1	Rbtn (*b*)	2	1
Ga	4	1	Rbsn	2	1
Gi	3	2	Sa	6	3
Goo (*a*)	1	1	Salb	4	2
Goo (*b*)	2	2	Sc (M)	3	1
Gr	1	3	Sc (P)	1	1
Ha (P)	5	2	Schm	6	2
Har	2	1	Shee	3	2
He	2	1	Sheld	1	1
Hi	2	1	Sm	0	1
Hu	2	1	Smi (B)	4	1
Hun	3	1	Smoth	3	1
Is	8	1	Spra	2	1
J (M)	3	1	Stream	1	1
J (R)	6	2	Sul	3	1
Joh	3	2	T	3	1
Jon	1	2	Tay (R)	7	1
Ka	3	1	Tenn	2	1
Kei	3	1	Terw	3	1
Kel	5	1	Warn	2	1
Ken	3	1	Web (H)	4	1
L	4	1	Weim	1	1
Li	7	2	Wh (E)	2	1
Mac	5	1	Wh (H)	2	1
McNab	4	1	Wilh	4	1
McPh	4	1	Wr	4	1
Ma	3	1			
				138	116

[14] The percentage of left-handed children is 45.67. According to Mendelian rules the expectation is 25 per cent. As noted before it is apparent that many of the parents reported as right-handed are really left-handed. Hence the large excess of left-handed children.

In the above ratios *RR* is pure right-handed, *Rr* is heterozygous right-handed and *rr* is left-handed. I have taken these particular proportions because they are stable and they approximate to a degree the actual condition in the population studied. As is noted in the table, the number of left-handed persons is probably greater than the reports indicate. Some families reported as having both parents right-handed evidently belong with the group of one left-handed and one right-handed. Some reported in this latter group belong, no doubt, with those having both parents left-handed.

TABLE V

ONE PARENT RIGHT-HANDED, THE OTHER LEFT-HANDED

A. Right-handed Parent Evidently Heterozygous (Families 36, Right-handed Children 88, Left-handed Children 55).

Name of Person Reporting	Right-handed Children	Left-handed Children	Name of Person Reporting	Right-handed Children	Left-handed Children
Ba.........	1	1	Li (*b*).......	1	1
Bi..........	2	1	McD.......	2	1
Br..........	2	1	McF.......	3	1
Bra.........	3	1	McK.......	3	1
Ca.........	3	4	Mal........	2	1
Ch.........	2	2	Mil.........	2	1
Cu.........	4	2	Mit.........	3	2
D'A........	0	1	Ols (*a*)......	1	1
Di..........	2	1	Ols (*b*)......	1	2
Fra.........	4	1	Or..........	0	1
Fre.........	1	1	Re.........	3	1
H (*d*).......	4	3	Ri..........	2	1
He.........	4	1	Str.........	2	1
Hea........	2	3	Wa (*a*)......	2	1
Hi..........	2	2	Wa (*b*)......	1	1
Ho.........	5	2	Web........	2	1
Kei.........	5	3	Wei........	5	2
Li (*a*).......	2	2	Wil.........	5	3
				88	55

Fecundity of Left-handed Families.—It is well known that in certain species of animals races showing particular recessive traits have less vitality and perhaps less reproductive ability than the ordinary members of the species. From the studies herein recorded, especially in Table II, it is seen that the left-handed families are quite as fertile as the normal ones.

Summary.—The foregoing pages are given to a study of left-handedness among 610 parents and 1,130 children, the data being collected from students at the University of Colorado. It is concluded that left-handedness is a Mendelian recessive. The condition probably exists in about one sixth of the population. A suggestion is made that the three Mendelian types of individuals may exist in some such proportion as 9 *homozygous right-handed*: 12 *heterozygous right-handed*: 4 *left-handed.*

B. Right-handed Parent Probably Homozygous (Families 9, Right-handed Children 27, Left-handed Children 0).

Name of Person Reporting	Right-handed Children	Left-handed Children	Name of Person Reporting	Right-handed Children	Left-handed Children
Ba	5	0	Nau	2	0
Be	4	0	Pi	3	0
Bl	1	0	Spr	2	0
Du	4	0	Sto	3	0
Mi	3	0			
				27	0

TABLE VI

BOTH PARENTS REPORTED AS LEFT-HANDED

Name of Person Reporting	Number of Right-handed Children	Number of Left-handed Children
McN	1	2
P	0	4
	1[15]	6

[15] Mendelian expectation requires that all the children of these families be left-handed. It is possible that one of the parents in the McN family was naturally right-handed and that the left-handedness was only acquired. If this is not the case then there seems no explanation to offer for the appearance of the right-handed child.

SUPPLEMENTARY STUDIES ON THE DIFFERENTIAL MORTALITY WITH RESPECT TO SEED WEIGHT IN THE GERMINATION OF GARDEN BEANS—II

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Comparison of Means

Take first the most stringent comparison—that between the constants of the seeds germinating normally and those of the seeds failing to germinate, *A–C*. The frequencies and mean magnitudes are:

	f	Absolute Values	Relative Values
Plus differences	29	+.396	+3.50
Minus differences	21	−.702	−4.62
All differences	50	−.065	+0.09

Or considering only differences which are at least 2.5 times their probable error:

	f	Absolute Values	Relative Values
Plus differences	15	+0.541	+5.42
Minus differences	9	−1.355	−8.84
All differences	24	−0.170	+0.07

For the 18 cases in which the differences are at least 4 times their probable errors the results are:

	f	Absolute Values	Relative Values
Plus differences	12	+0.536	+ 5.73
Minus differences	6	−1.634	−10.93
All differences	18	−0.187	+ 0.17

These facts in a somewhat different form are made clear to the eye in Diagrams 1 and 2.[14]

[14] Two types of graphs seem most suited to bring out clearly these results. In both, the signs and magnitudes of the differences between the normally developing and the eliminated series are shown by the direction and lengths of a series of lines. The solid lines falling below the zero bar show on the scale to the left the magnitude of the negative differences—*i. e.*, of those

The first of these graphs shows the values reduced to percentages of the constants for the general population of seeds from which the samples used in these experiments were drawn, *i. e.,* the constants given in Table X. The second shows the ratio of the differences to their probable errors.

The impression given by both of these charts is that the mean weight of the surviving seeds has been increased by the mortality, although there are one or two conspicuously large negative values in each case. This impression is borne out by the numerical result, if we confine our attention to the signs, merely. Of the 50 experiments, 29 show an increase and 21 a decrease in seed weight, whereas if there were no relationship between mean seed weight and viability, the deviations would be expected to be equally divided between positive and negative, except for the error of random sampling which would be given by $.6745 \sqrt{50 \times .5 \times .5}$. Thus in the present case for the whole fifty experiments, the deviation from the equality which we should expect if there were no relationship between mean seed weight and mortality is 4 ± 2.38 series. Surely this can not be regarded as a trustworthy difference, but we note that the difference has the same sign and is relatively larger as we reduce our number of cases by disregarding those comparisons which are less

in which the seeds failing were heavier or more variable than those which developed, in which selection decreased mean weight or variability. The broken lines extending above the zero bar show the number and the magnitude of the differences indicating an increase in mean or in variability as the result of selective elimination. The length of these bars may be determined in three different ways. They may simply represent the absolute differences (in units of .025 gram). They may represent percentage difference, on the basis of the constant for the whole population, as explained above. They may be in terms of the ratio of the difference to its probable error.

The first is the method used in the diagrams of the earlier paper. It is of no advantage here where the number of entries is too numerous to enable absolute values for individual series to be conveniently read from them. The second has the merit of presenting to the eye all the values in comparable terms. The third shows at a glance the statistical significance to be attached to the differences represented. The two latter are used.

probably statistically significant with respect to their probable errors. Thus if we throw out the 26 cases which are less than 2.5 times their probable error, we find that 15 are positive and 9 negative, a deviation of 3 ± 1.65.

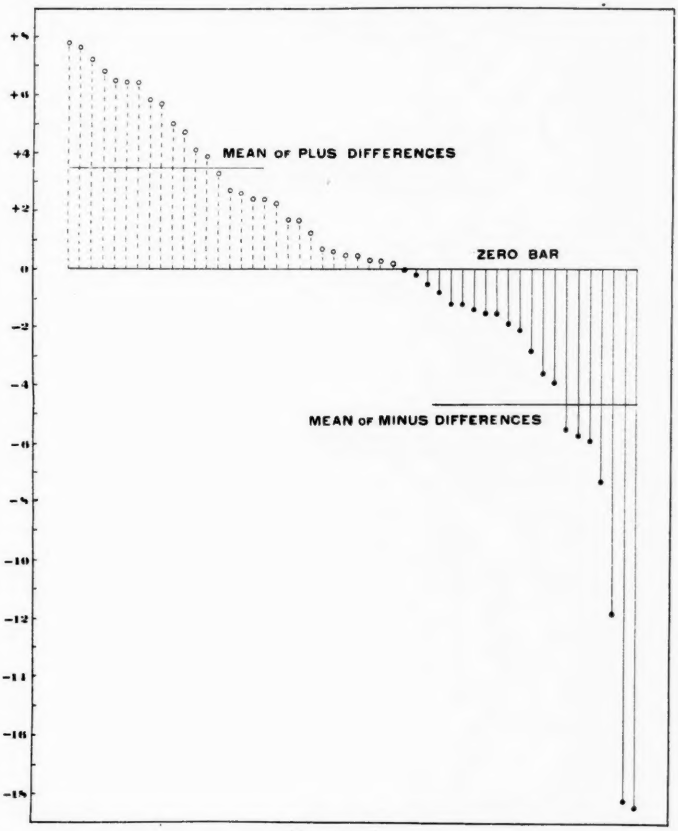

DIAGRAM 1.

If we consider only differences which are four times their probable error, we find 12 positive and 6 negative, a deviation from equality of 3 ± 1.43.

When, however, we turn to the averages—both absolute and relative—we see very little support for the view that there is a tendency for the weight of surviving seeds

to be heavier than those which fail. Sometimes, the general average is positive and sometimes it is negative in sign; it is always insignificant in magnitude. Nor, to

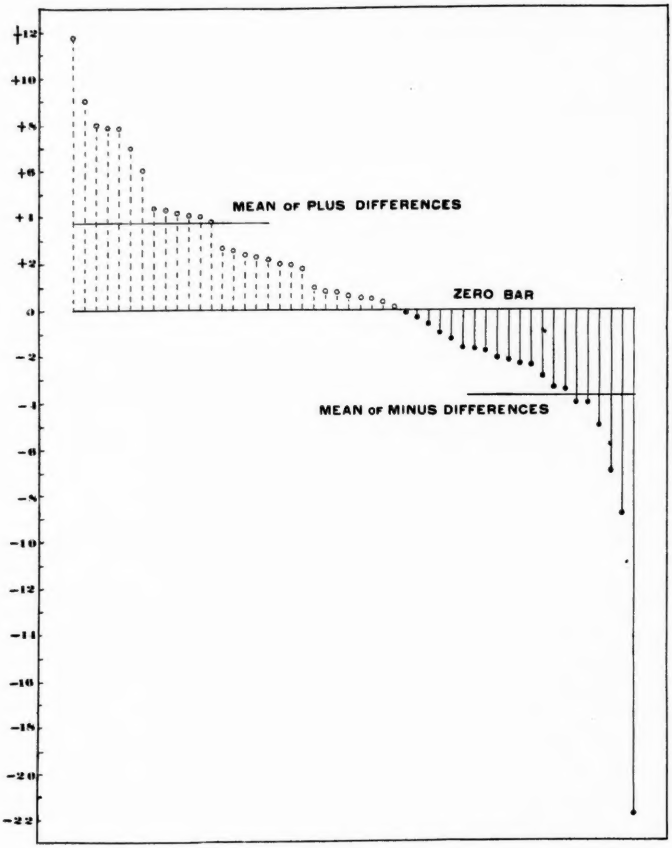

DIAGRAM 2.

return to the question of the more qualitative classification of the experiments, can any great weight be attached to such inequalities in the number of positive and negative differences as we have secured.

The mean values of the ratios of the differences, $A-C$, to their probable errors have also been struck. The 21

negative cases give a mean ratio of 3.70 while the 29 positive values give 3.75. These substantial averages taken in connection with the number of rather high individual ratios certainly suggest that there are real biological differences between the samples of seeds. One expression of these differences is seen in the fact that in some cases the seeds which survive average heavier and in other cases lighter than in the population from which they were drawn.

Consider now the weight relations of seeds giving abnormal germinations and those failing to germinate, *B–C:*

	f	Absolute Values	Relative Values
Plus differences	32	+.581	+4.34
Minus differences	18	−.287	−2.08
All differences	50	+.268	+2.03

Thus there is a deviation from equality of 7 ± 2.38 cases, and this is probably significant.

For the abnormal germinations N is small; there are only 12 cases in which the difference is over 2.5 times its probable error. These are:

	f	Absolute Values	Relative Values
Plus differences	11	+1.026	+7.39
Minus differences	1	−0.450	−2.23
All differences	12	+0.903	+6.58

In seven series, diff. $E_{\text{diff.}} > 4$. *All these are positive;* they give a mean of 1.093 *absolute* and 8.47 *relative.*

Thus, apparently, the seeds which germinate abnormally are distinctly heavier than those which fail to germinate.

If now we combine A and B and compare all seeds which germinated with all those which failed, we have:

	f	Absolute Values	Relative Values
Plus differences	31	+0.360	+3.25
Minus differences	19	−0.513	−3.26
All differences	50	+0.028	+0.77

For the cases which are 2.5 or more times their probable error:

	f	Absolute Values	Relative Values
Plus differences	17	+0.510	+4.92
Minus differences	7	−1.035	−6.44
All differences	24	+0.060	+1.60

Thus by combining normal and abnormal germinations there is stronger evidence for an increase in mean seed weight by a selective death rate than when the normal germinations alone are considered. This point will be taken up again.

Just here it is necessary to point out that in this series merely the capacity for germination of the seeds in sand is taken into account, whereas in the former study only those were considered viable which had produced fertile plants. In combining normal and abnormal seedlings and contrasting them with those which failed to germinate at all, we are undoubtedly considerably overestimating the capacity for survival in nature.[15]

[15] From personal experience in the handling of the plants I have no doubt whatever that had germination taken place in a substratum less easily displaced than sand (*e. g.*, in a stiff clay soil) a number of the seeds classified as abnormal in germination would not have succeeded in unfolding their primordial leaves to the light. Again, I believe there is not the slightest question that of those which did reach the surface a higher proportion would fail to develop into mature plants than of the seedlings classified as normal. In fine, there is probably a post-germination as well as pre-germination mortality, and this mortality is probably selective. Indeed for morphological variations it has been shown to be so. (Harris, J. Arthur, "A Simple Demonstration of the Action of Natural Selection," *Science*, N. S., 36: 713–75. 1912). My general impression from working with the seedlings of both sorts is that there is likely to be a larger difference in mortality between the normal and abnormal seedlings of this paper than between the normal and abnormal seedlings of the study of the death rate of normal and morphologically aberrant seedlings.

It is possible, therefore, that such differences in mean weight as are found between the results of the two investigations may be in part due to a somewhat different elimination during germination and in part due to a selective mortality occurring beyond the point at which the census for the later series of experiments was necessarily closed. Thus it appears that when the abnormal germinations are grouped with the normal to give the comparison $(A + B) - C$ the evidence for an increase in mean seed weight through selective mortality of the lighter seeds is strengthened. A comparison of the two classes of seedlings also suggests that the seeds giving rise to those which are abnormal may be heavier than those germinating

Ideally, to obtain results valid for individuals attaining reproductive maturity one should take a small proportion of the seeds germinating normally and a much higher proportion of those giving rise to abnormal seedlings and combine them with the seeds failing to germinate. There is no possible way of estimating the proportion of A and B which should be classed with C. If one wishes to make the comparison which shall be at the opposite extreme of that in which all seeds germinating at all are compared with those failing to germinate, he may combine the seeds germinating abnormally with those which do not germinate. Thus $(A+B)-C$ and $A-(B+C)$ will give us the upper and lower possible measures of the influence of mortality of abnormal seedlings on seed weight.

Turning to the comparison of means for $A-(B+C)$:

	f	Absolute Values	Relative Values
Plus differences	27	+0.371	+3.46
Minus differences	23	−0.745	−4.81
All differences	50	−0.142	−0.35

Restricting comparisons to differences at least 2.5 times their probable error:

	f	Absolute Values	Relative Values
Plus differences	14	+0.524	+5.28
Minus differences	13	−1.192	−7.73
All differences	27	−0.302	−0.99

Or restricting still further to those which are at least $4E$:

	f	Absolute Values	Relative Values
Plus differences	12	+0.515	+ 5.46
Minus differences	8	−1.599	−10.64
All differences	20	−0.331	− 0.98

Certainly, there is in these figures no trustworthy indication of an increase of mean weight as a result of selective mortality.

normally. If this is true, and if the abnormal seedlings have a higher post-germination mortality, it is clear that some of the increase in mean observed in these experiments would have disappeared if the plants had been required to develop to maturity under field conditions.

Somewhere between this minimum value and the one given above by $(A + B) - C$ probably lies the true measure of the change in mean weight as it would occur if the plants were required (as they would be in nature) to grow to reproductive maturity.

I now turn to the individual varieties. This demands, for results which shall be at all trustworthy, the combination of both sets of experiments.[16]

The accompanying table gives the results for the relative differences in mean weight (differences expressed as percentages of the general population constant).

Varieties	f	Relative Values
NAVY:		
Plus differences	18	+2.461
Minus differences	6	−1.134
All differences	24	+1.562
NE PLUS ULTRA:		
Plus differences	5	+1.122
Minus differences	3	−1.962
All differences	8	−0.022
WHITE FLAGEOLET:		
Plus differences	9	+1.787
Minus differences	3	−0.247
All differences	12	+1.276
BURPEE'S STRINGLESS:		
Plus differences	10	+1.244
Minus differences	16	−1.048
All differences	26	−0.167
GOLDEN WAX:		
Plus differences	0	——
Minus differences	7	−2.087
All differences	7	−2.087
FLAGEOLET WAX:		
Plus differences	1	+0.263

[16] The method of rendering the result of these sand cultures most nearly comparable with the field experiments is to draw the comparison between the germinated seed and the general population from which they were drawn. Of course, the errors of random sampling in the drawing of the seeds would be overcome by comparing the constants for the seeds actually planted $(A + B + C)$ with those failing to develop, but this would not give differences comparable with those from field culture work where $(A + B + C + \ldots)$, not $(A + B + C)$, is known.

Anyone who cares to do so may make this comparison numerically for the whole material by taking the physical constants for $(A + B)$ and subtracting from them the general population constants given in Table X. It has already been made graphically in a paper on "Current Progress in the Study of Natural Selection," in *Pop. Sci. Mo.*, in press.

I believe that the purely statistical differences between the two sets of

This anaylsis of means by varieties is most suggestive. Leaving out of account Flageolet Wax for which there is only a single experiment, it appears that in Navy and White Flageolet there is a distinct increase in mean weight of survivors, that in Ne Plus Ultra and Burpee's Stringless there is no marked change in mean weight, while in Golden Wax there is a pronounced tendency for the survivors to be lighter than the general population.[17]

It is clear that such a condition as this would give, with a proper combination of strains, precisely the general result that we have found for the means: that is, an average of no change by selective elimination but significantly positive differences in some experiments and significantly negative differences in others. Here is a problem requiring further analysis—which, however, can be profitably undertaken only when larger bodies of experimental evidence are at hand.

Comparison of Absolute Variabilities

For the standard deviations for seeds germinating normally and seeds failing to germinate, *A–C*, in the whole material the results are:

experiments are not sufficient to be of material importance. Much greater weight is probably to be attached to certain experimental and biological factors. These are to be seen in both (*a*) the possible influence of the two types of substrata, and (*b*) the fact that in the field cultures viability was measured in terms of capacity to produce mature fertile plants, while in the sand cultures it was (necessarily) measured in terms of the capacity for (normal or abnormal) germination only.

[17] Possibly these results are due merely to the unavoidable errors of experiment and of sampling. Only far wider series of data can settle this point; until then no stress whatever is to be laid upon it. But *a priori* there is nothing unreasonable or improbable in such results. These varieties differ widely in the characteristics of their seeds and there is nothing surprising in the indication that in one variety the death rate is more concentrated toward the lower end of the range of variation, in another it is more restricted to the upper limit, while in a third both extremes are decimated. This seems especially probable in view of the fact that in this as in other cultivated species the varieties have been developed to suit the fancy of man and not to meet the requirements of the race in competitive life in nature.

	f	Absolute Values	Relative Values
Plus differences	17	+.145	+ 8.67
Minus differences	33	−.351	−13.77
All differences	50	−.183	− 6.14

These relationships are made clear by Diagrams 3 and 4. The first of these shows the differences in standard deviations expressed as percentages of the population S.D. The second shows the ratio of the differences to their probable errors.

The distribution of the differences which are at least 2.5 times their probable errors may be summarized:

	f	Absolute Values	Relative Values
Plus differences	5	+.335	+21.81
Minus differences	15	−.569	−21.64
All differences	20	−.343	−10.78

Thus of the 17 positive differences, 12 or about 71 per cent. are statistically untrustworthy (*i. e.*, $< 2.5E$) while

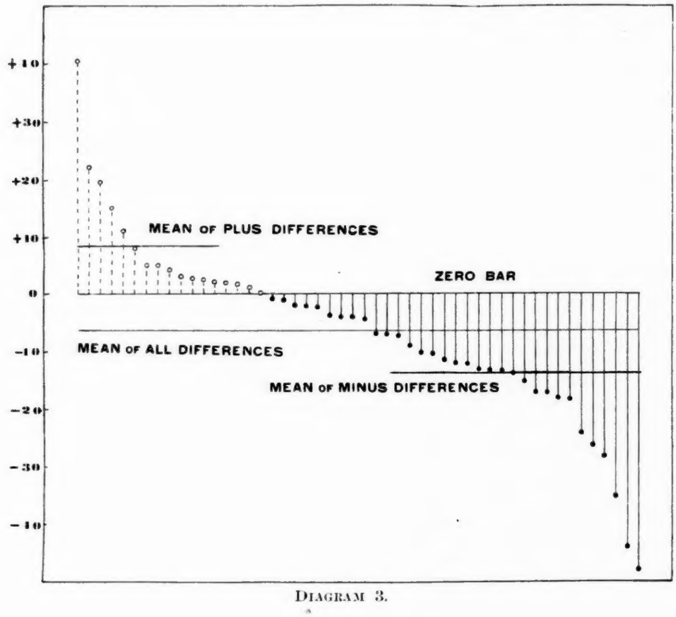

DIAGRAM 3.

of the 33 negative differences, only 18 or roughly 55 per cent. are not statistically significant. The deviations from equality are 8 ± 2.38 for the whole material and 5 ± 1.51 for the 20 series which are more probably statistically significant.

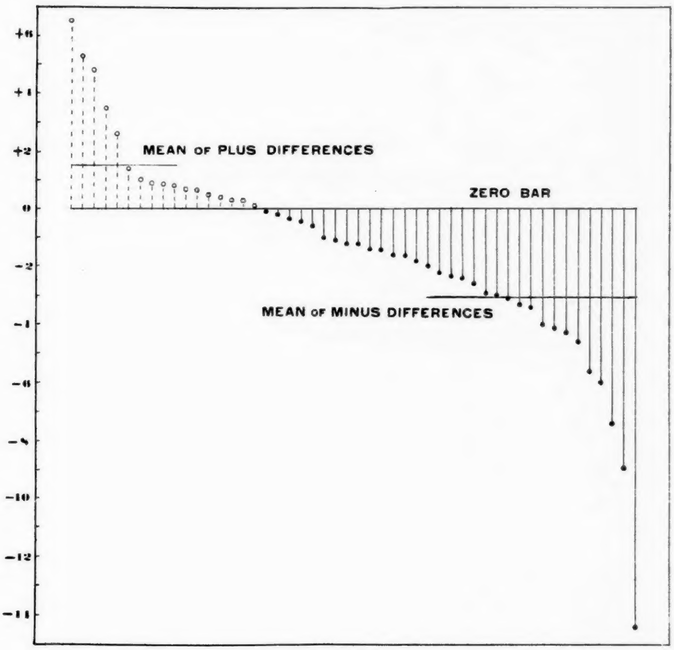

DIAGRAM 4.

Only 12 individual differences are over four times their probable error:

	f	Absolute Values	Relative Values
Plus differences	3	+.363	+25.22
Minus differences	9	−.769	−27.31
All differences	12	−.486	−14.18

These results can leave no doubt as to the reduction in the absolute variability when the seeds which produce normal seedlings are selected out from those which fail

to develop. The number of negative differences is significantly higher than the number of positive differences. The mean of the negative differences is larger numerically than that of the positive differences. The proportion of negative differences is higher among the constants which are more probably trustworthy, being only 1.5 : 1 among those $< 2.5E$ but 3 : 1 among those $> 2.5E$. The average ratio of the difference to its probable error is only 1.65 for the positive differences, but reaches 3.04 for those which are negative in sign.

Thus these results are in excellent agreement with those of the field experiments.

Turn now to the same question with regard to the seeds giving abnormal germinations, *B–C:*

	f	Absolute Values	Relative Values
Plus differences	23	+.235	+12.14
Minus differences	27	−.331	−15.32
All differences	50	−.071	− 2.69

For those differences at least 2.5 times their probable error, the results are:

	f	Absolute Values	Relative Values
Plus differences	3	+.466	+28.14
Minus differences	11	−.501	−21.75
All differences	14	−.294	−11.06

Perhaps the evidence for a reduction in variability is not so strong when seeds germinating abnormally are compared with those not germinating at all. This is precisely what one would expect if such seeds may be regarded as in some degree intermediate between those which produce perfect seedlings and those which produce no seedlings at all.

I now turn to the question of a possible reduction in variability as one passes from seeds germinating abnormally to those germinating normally. The answer is given by the comparison *A–B:*

	f	Absolute Values	Relative Values
Plus differences	19	+.273	+13.78
Minus differences	31	−.366	−15.95
All differences	50	−.123	− 4.66

For differences 2.5 or more times their probable errors:

	f	Absolute Values	Relative Values
Plus differences	6	+.505	+24.41
Minus differences	9	−.560	−25.08
All differences	15	−.134	− 5.29

It is clear that in passing from the seeds producing abnormal seedlings to those germinating normally there is in general a reduction in absolute variability of weight. This point will be discussed in greater detail when relative variabilities are taken up.

If now the comparisons be drawn between all seeds which germinate (whether normally or abnormally) and those which do not germinate at all, *i. e.*, $(A+B)-C$, we have:

	f	Absolute Values	Relative Values
Plus differences	15	+.136	+ 8.37
Minus differences	35	−.266	−11.18
All differences	50	−.146	− 5.32

Or restricting the comparison as usual to those which are more probably statistically trustworthy $(>2.5E)$:

	f	Absolute Values	Relative Values
Plus differences	4	+.297	+20.85
Minus differences	13	−.475	−19.12
All differences	17	−.294	− 9.72

The comparison involving the other extreme in the treatment of the abnormal seedlings is $A-(B+C)$. For all the series this gives:

	f	Absolute Values	Relative Values
Plus differences	17	+.160	+ 9.13
Minus differences	33	−.331	−13.45
All differences	50	−.164	− 5.77

For cases at least $2.5E$, the results are:

	f	Absolute Values	Relative Values
Plus differences.	5	+.352	+22.21
Minus differences.	16	−.521	−20.26
All differences.	21	−.312	−10.15

Thus the treatment of the abnormal germinations does not materially affect the general results for reduction in variability.

It seems unnecessary to consider both absolute and relative variabilities for the individual varieties. The results will be summarized for the coefficients of variation.

Comparison of Relative Variabilities

As demonstrated in the preceding sections, mortality is so related to seed weight that absolute variability is reduced in passing from seeds which fail to germinate to those which produce seedlings. Possibly, too, there is a change in type. Such changes in mean, even if due only to the errors of sampling, may somewhat affect absolute variabilities. It is desirable, therefore, to reduce all these to relative terms—to express them as ratios of the absolute variabilities ($\times 100$) to the means.

The coefficients of variation, being already in relative terms, give only one set of means to consider.

For *A–C*, all series, the results are:

	f	Averages
Plus differences.	12	+1.45
Minus differences.	38	−1.95
All differences.	50	−1.13

Thus we have a deviation from the 25:25 ratio of 13 ± 2.38 which must certainly be regarded as significant.

For cases at least 2.5 times their probable error:

	f	Averages
Plus differences.	3	+3.45
Minus differences.	16	−3.26
All differences.	19	−2.22

Only 8 are 4 or more times their probable error. Of these, 3 are positive, averaging $+3.34$, while 5 are negative, averaging -4.45.

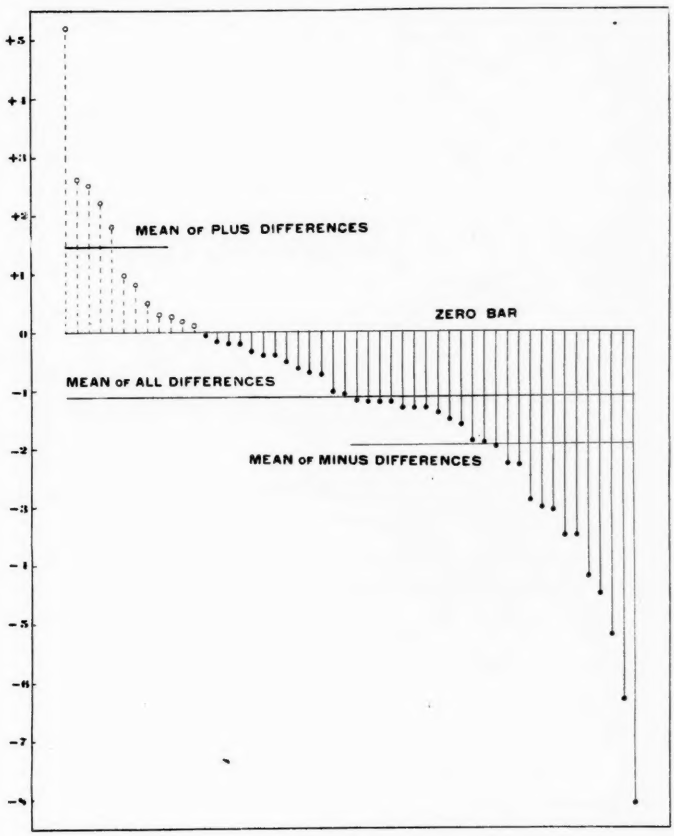

DIAGRAM 5.

The differences for *A–C*, all material, are shown in Diagram 5. Note by comparison with Diagrams 3 and 4 that the evidence for selective mortality becomes stronger when variabilities corrected for size of the means are substituted for absolute values.

Comparison of the relative variability in weight of seeds giving abnormal germinations with that of those failing to germinate at all, *B–C*, gives:

	f	Averages
Plus differences..................	18	+2.24
Minus differences................	32	−2.35
All differences....................	50	−0.70

Restricting comparisons to differences at least $2.5E$:

	f	Averages
Plus differences..................	2	+5.47
Minus differences................	10	−4.74
All differences....................	12	−3.04

Differences at least $4E$ are:

	f	Averages
Plus differences..................	1	+6.17
Minus differences................	6	−4.56
All differences....................	7	−3.03

The reduction in variability in passing from *C* to *B* is clearly significant.

Consider now the difference between seeds germinating abnormally and those germinating normally, *A–B*:

	f	Averages
Plus differences..................	21	+2.11
Minus differences................	29	−2.27
All differences....................	50	−0.43

Or taking the usual minimum standard of statistical significance:

	f	Averages
Plus differences..................	7	+3.42
Minus differences................	5	−5.32
All differences....................	12	−0.23

There is no certainty of any reduction in relative variability here. But turning back to the standard deviations we find that there were fair indications of a lowering of variability.

This apparently contradictory result finds an explanation when the means are taken more fully into account. Consider these, *A–B:*

	f	Absolute Values	Relative Values
Plus differences	23	+.331	+2.96
Minus differences	27	−.899	−5.96
All differences	50	−.333	−1.86

Restricting to those at least 2.5*E:*

	f	Absolute Values	Relative Values
Plus differences	6	+0.596	+ 5.43
Minus differences	12	−1.703	−11.02
All differences	18	−0.937	− 5.54

The mean weights are higher in series *B* than in series *A. The relative variabilities for B are, therefore, reduced by the higher values of the means.* Thus when we take the comparison *A–B* for relative variabilities, the reduction which we noted in dealing with the absolute values does not appear.

Consider now the result of combining all seeds which germinated at all (whether normally or abnormally) and comparing their coefficients of variation with those of the seeds which failed to germinate, $(A+B)-C$:

	f	Averages
Plus differences	12	+1.29
Minus differences	38	−1.71
All differences	50	−0.99

Or restricting to differences at least 2.5*E:*

	f	Averages
Plus differences	4	+2.74
Minus differences	13	−2.69
All differences	17	−1.41

Thus we have for all the material a deviation of 13 ± 2.38 cases from the equality to be expected if there were no selective mortality tending to reduce variability. In 38 cases out of 50 the variability of the seeds which germinated is lower than that of those which failed.

In this comparison, all seeds which germinate at all have been considered viable—although it is practically certain that many of the abnormal ones would not have been able to reach maturity. If one wishes to take the other extreme, he may throw all the seeds producing abnormal seedlings with those which failed to germinate at all and compare with those germinating in a perfectly normal manner, $A-(B+C)$.

	f	Averages
Plus differences	12	+1.52
Minus differences	38	−1.69
All differences	50	−0.92

Or for differences $>2.5E$:

	f	Averages
Plus differences	4	+3.13
Minus differences	16	−2.65
All differences	20	−1.49

Thus the disposition of the abnormal seedlings makes relatively little difference in the end result.

Variety	f	Mean Difference
Navy:		
Plus differences	9	+1 253
Minus differences	15	−0.796
All differences	24	−0.028
Ne Plus Ultra:		
Plus differences	4	+0.878
Minus differences	4	−1.833
All differences	8	−0.478
White Flageolet:		
Plus differences	2	+0.031
Minus differences	10	−0.683
All differences	12	−0.563
Burpee's Stringless:		
Plus differences	3	+0.637
Minus differences	23	−0.669
All differences	26	−0.518
Golden Wax:		
Plus differences	1	+0.175
Minus differences	6	−1.356
All differences	7	−1.137
Flageolet Wax:		
Minus differences	1	−0.283

I now combine the differences $(A+B)-(A+B+C+\cdot\cdot\cdot)$ for the 50 experiments of the present paper

with the 28 given by the field test, as already done for the relative means. The little table gives the results.

For every variety except Ne Plus Ultra the differences are exclusively or preponderantly negative. For each of the six varieties the general average is negative in sign, although sometimes very low. Such results give additional force to the conclusion that there is a reduction in variability due to a differential mortality.

V. Recapitulation and Discussion

1. This paper embodies a portion of the data of a second study of the relationship between seed weight and seed viability in *Phaseolus vulgaris.* The constants are based on greenhouse plantings in sand of some 46,000 individually weighed seeds, chiefly of the pedigrees employed in the field experiments.

Bearing in mind the various sources of error sufficiently emphasized in the body of the paper, the following may be said of the findings.

2. In general the results of the first study are fully confirmed. In certain particulars, however, the narrower analysis made possible by the wider materials now available suggests some modification and considerable extension of conclusions.

3. The statement concerning means was:

> This selective death rate is of such a nature that the mean of the available seeds remains practically the same as that of the original populations, while the variability is reduced. In short, both large and small seeds are less capable of developing into fertile plants than are those which do not deviate so widely above or below the type.

This was all that could then be said, for while many thousands of individually weighed seeds were involved, the number of series was too low to justify analysis into the individual varieties or into groups by age of seed or conditions of growth. Examined in the same manner, these data show *in the long run* some indication of an increase in the mean weight of the survivors, but no un-

controvertible evidence of a change in mean weight as a result of selective mortality. But *individually considered*, more differences in mean weight are from two to four or more times their probable errors than can possibly be attributed to experimental or sampling errors. Some of these differences are positive, others are negative. There seems in view of these facts, no escape from the conclusion that there is a real biological relationship between weight and viability of such a nature that in some experiments the heavier and in other experiments the lighter seeds are most heavily drawn upon in the mortality. This seems clear from the greenhouse experiments in whatever way the differences are taken. There are indications of the same condition in field cultures, although here the criterion of statistical trustworthiness is, because of the dual errors of sampling, less dependable.

There is strong evidence for varietal differences with respect to mortality. In some strains the heavier, in others the lighter, seeds seem less capable of development. The reason for these differences may be sought in the inherent characters of the stocks used or in the environments to which they have been subjected. This question is, however, so complicated that larger and more diverse series of data must be gotten together for its final solution.

4. Consider now the variabilities. There can be no question whatever concerning the reality of the reduction in variability, either absolute or relative, as a result of differential mortality. The following conditions seem to prevail for the individual comparisons which may be made.

There is probably a reduction in absolute variability, and there is certainly a reduction in relative variability, in passing from seeds which fail to germinate to those which produce abnormal seedlings.

There is probably also a reduction in standard deviation in weight in passing from seeds which give abnormal seedlings to those which germinate normally. This re-

duction is not so evident in the coefficients of variation, probably because of changes occurring in mean weight.

There is clearly a lowering of both absolute and relative variabilities between seeds which fail to germinate and those which germinate normally, or those which germinate at all, either abnormally or normally. The disposition which is made of the seeds which give rise to abnormal seedlings does not affect the conclusion concerning a reduction in variability due to a differential death rate.

To what extent this reduction is incidental to a change in mean through elimination preponderantly from one end of the range, as compared with elimination from both the extremes without change of type, must be determined on wider series of data, and probably by the use of statistical methods not yet applied to the problem.

5. The constants of this paper, taken in connection with data made directly available from other published studies by the key letters, can be used towards the solution of a number of problems not touched upon here. These have been purposely left out of account because they were aside from the present main purpose and because I hope to have much more extensive materials for their solution later.

6. Concerning the causes of the differences in viability no conclusions can be drawn. I have shown[18] that in general the larger seeds require longer for germination, but the precise relation, if any, of this phenomenon to selective mortality, as well as its explanation in more general physical and chemical terms, are still to be worked out.

TUMAMOC HILL, TUCSON, ARIZ.,
April 3, 1913

[18] Harris, J. Arthur, "A First Study of the Relationship between the Weight of the Bean Seed, *Phaseolus vulgaris*, and the Time Required for its Germination." In press.

SHORTER ARTICLES AND DISCUSSION

A CROSS INVOLVING FOUR PAIRS OF MENDELIAN CHARACTERS IN MICE

THE present experiment was planned as a control upon more detailed work being carried on at the Bussey Institution. It has, however, a distinct value, as demonstrating from a single cross the existence of four independent pairs of Mendelian characters in the color inheritance of mice.

That the yellow and agouti factors are not inherited independently of each other has been demonstrated by Sturtevant.[1]

The four pairs of characters under consideration here were recorded by Castle and Little[2] and are briefly as follows:

A = agouti, a = non-agouti.
B = black, b = no black (brown).
D = density, d = diluteness.
P = dark eye, p = pink eye.

In each case the character represented by the small letter is recessive in combination with its allelomorph, designated by a large letter.

To obtain all possible combinations of these four pairs of characters, a single pure wild gray mouse was mated with several pink-eyed dilute brown females from a homozygous stock bred at the Bussey Institution and shortly to be reported upon by one of the writers.

Wild gray mice possess the dominant members of all four paired characters mentioned above, and consequently have the gametic formula ABDP. The pink-eyed dilute brown mouse, on the other hand, exhibits the recessive conditions of the same factors and is of the formula abdp. It is in appearance a very pale lilac color and in Miss Durham's classification is described as "Silver Champagne."[3]

The F_1 individuals resulting from this cross (wild ♂ × pink-eyed dilute brown ♀) were all, as expected, similar to the wild

[1] AM. NAT., 1912, p. 368.
[2] *Science*, 1909, p. 312.
[3] *Journal of Genetics*, 1911, p. 159.

parent in color. They were mated *inter se* and disposed so as to raise as large a number of F_2's as possible.

In this F_2 generation we should expect to find sixteen visibly different types of color, in the proportions indicated in Table I. Table I also shows the results actually obtained in the experiment.

TABLE I

Color	Formula	Observed Numbers	Expected Numbers	Theoretical Proportion	Observed Proportion
Black Agouti	ABDP	436	373.4	81	94.5
Black	aBDP	127	124.5	27	27.5
Brown Agouti	AbDP	103	124.5	27	22.3
Dilute Black Agouti	ABdP	130	124.5	27	28.2
Pink Eyed Black Agouti	ABDp	103	124.5	27	22.3
Brown	abDP	40	41.5	9	8.7
Dilute Brown Agouti	AbdP	31	41.5	9	6.7
Dilute Black	aBdP	37	41.5	9	8.0
Pink Eyed Black	aBDp	35	41.5	9	7.6
Pink Eyed Brown Agouti	AbDp	38	41.5	9	8.2
Pink Eyed Dilute Black Agouti	ABdp	38	41.5	9	8.2
Dilute Brown	abdP	11	13.8	3	2.4
Pink Eyed Brown	abDp	12	13.8	3	2.6
Pink Eyed Dilute Brown Agouti	Abdp	15	13.8	3	3.3
Pink Eyed Dilute Black	aBdp	17	13.8	3	3.7
Pink Eyed Dilute Brown	abdp	7	4.6	1	1.5
Total		1,180			

If we consider each allelomorphic pair of characters separately, the following results are observed (Table II):

TABLE II

Characters	Observed Numbers	Expected Numbers	Theoretical Proportions	Observed Proportions
A	894	885	3	3.12
a	286	295	1	1
B	923	885	3	3.59
b	257	295	1	1
D	894	885	3	3.13
d	286	295	1	1
P	915	885	3	3.45
p	265	295	1	1

It will be seen that there is in each case a slight excess of animals possessing the dominant character. Further, in Table I there was an excess of black agouti (gray) animals, which possess all four dominant characters.

This last excess, however, is not sufficient, in the opinion of the writers, to support any theory of coupling, especially in the absence of significant differences in the other classes.

The excess of grays may better be explained on the basis of selective elimination of the various recessive animals, for the F_2 young could not be graded satisfactorily until nearly four weeks old, and no account was kept before this time.

A minor error may have occurred in recording the pink-eyed dilute brown young, as they resemble closely the intense pink-eyed brown and no breeding test was undertaken.

To summarize the results of this mating, it is obvious that we are dealing with four clear-cut pairs of Mendelian characters as described by Castle and Little in 1909, among which no coupling or association can be detected.

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